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Construction principles and control over transport systems organization in biological tissues

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Abstract

The main common principles of the long-range transport systems construction in animal and plant tissues are summarized. The results of measurement of conducting system geometry in Cotinus obovatus leaf are analyzed. It is shown that the principles of design of the conducting systems in animals and higher plants are the same and correspond to the model of optimal pipeline. The mathematical model of fluid motion in the conducting system of the leaf as a mo tion in a branching pipeline with permeable walls is investigated. The cost of a bifurcation of the vessels is analyzed. The hypothesis of the control principle of optimal transport system formation in the growing leaf is discussed. As an example the self-similar conducting system with loops is investigated and compared with some venation systems in plant leaves.

1. Principles of transport systems construction

Special conducting structures in biological systems are designed for transport of a liquid and dissolved substances on the distances comparable to the characteristic size of the biosystem. In higher plants and animals the conducting structures are represented by the branching vessels networks with 5-9 orders of branching in plant leaves and above 20 orders in mammalian arterial and venous systems. In spite of the complicated topology of the networks the simple rulers of their organization were found out in experiments and measurements. Laws of the vascular systems organization are investigated with the help of special casts, radiographic, x-ray images and tinted preparations. The lengths L_i, diameters D_i and branching angles α_i (Fig.1) at each bifurcation as well as the number of vessels N_i of the same order i are measured. The order of branching i is determined as follows:

1. The first (largest) vessel has $i=1$;

2. Two vessels with the orders l and k join into the parent vessel with the order

$$i=\begin{cases} l+1 & at \quad l=k \\ \max\{l,k\} & at \quad l\neq k \end{cases}$$

The following statistical dependences between the measured parameters were obtained for the arterial [1–4,6], venous [1,2,3], respiratory [1,6,7] mammal systems, astrorhizal systems in sponge [1], tree trunks and shoots [8-9], plant leaves of different types [10-11]:

1. $D_{j0}^g = D_{j1}^g + D_{j2}^g$ (Murray's law), where $D_{j0,1,2}$ – the diameters of the parent and daughter's vessels at the bifurcation j. For the most networks $g \approx 3$ ($g=2.55-3.02$ for arterial, $g=2.76-3.02$ for venous, $g=2.61-2.91$ for respiratory systems) and the higher the animal's position at the evolutionary scale, the closer g to 3 [12]. For the large vessels where flow is not laminar (aorta, respiratory trunk) $g \sim 2.33$ was obtained [5]. For the small vessels where the fluid rheology should be taken into account $g \sim 2.92$;

2. $$\cos(\alpha_{j1}) = \frac{(1+x_j^3)^{4/3}+1-x_j^4}{2(1+x_j^3)^{2/3}}$$

$$\cos(\alpha_{j2}) = \frac{(1+x_j^3)^{4/3}+x_j^4-1}{2x_j^2(1+x_j^3)^{2/3}}$$

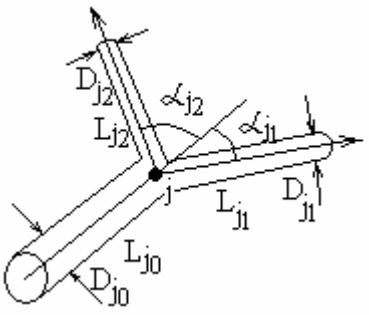

Figure 1: Geometry of the vascular bifurcation.

where $x_j = D_{j2}/D_{j1}$ – asymmetry of the bifurcation;

3. $$N_i = a_1 D_i^{-b_1}, \quad L_i = a_2 D_i^{b_2} \qquad (1)$$

where $a_2, b_{1,2}$ characterize the network structure, a_1 - a scale multiplier. For mammalian arterial beds $a_2 = 2.60–7.59$, $b_1 = 2.15–2.76$, $b_2 = 0.84–1.16$. Because of the $b_2 \sim 1$ and $L_i \sim a_2 D_i$, the Murray's law for the vessels' lengths at a bifurcation is valid.

4. Fractal dimensions l of the transport systems of quite different nature are similar [13-14]: $l = 1.537 \pm 0.036$ for the arterial and $l = 1.532 \pm 0.03$ for the venous vessels of the retina [15], $l = 1.737 - 1.844$ for the respiratory arterial system. The value $l = 1.6$ is peculiar to the biological and non-biological so-called reaction-diffusion systems;

5. The geometrical parameters of the conducting systems correspond to the model of the optimum branching transport system providing delivery of a liquid at the minimal total cost [1,2,3,5,7,11].

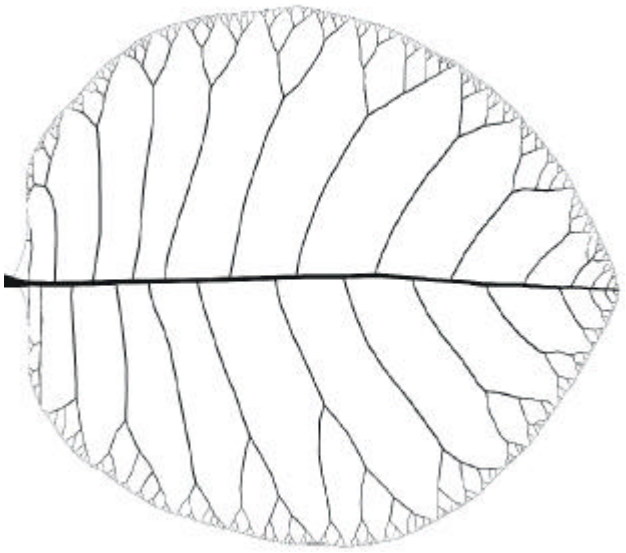

Figure 2: *Cotinus obovatus* leaf venation.

2. Transport system organization in plant leaves

In the present article some results of the *Cotinus obovatus* leaves (Fig.2) conducting system investigation are presented. The geometrical parameters $L_{j,0-1}$, $D_{j,0-1}$ of conducting system were measured on the scanned images of the green leaves using image analysis software (SciImage 3b). The total number of elements of each branching order $i = 1-5$ was calculated. The dependences $N_i = N_i(D_i)$ and $L_i = L_i(D_i)$ were obtained in form (1) and the corresponding coefficients $a_{1,2}$, $b_{1,2}$ were calculated with least squares method. As an illustration the dependence $L_i = L_i(D_i)$ for one leaf (approximately 200-250 vein bifurcations) is represented in Fig.3. Two subsystems can be distinguished: the system of the so-called distributed vessels (relatively large veins $i = 1-2$) with $b_2 = 3.2$ and the delivering vessels (minor veins $i = 3-5$) with $b_2 = 1.6$ (Fig.3). The same subsystems were found in coronary arterial system [16]. The function of the distributing veins is to convey the fluid into different zones of the leaf blade, while the function of the delivering veins is to provide uniform delivering the fluid into each cell.

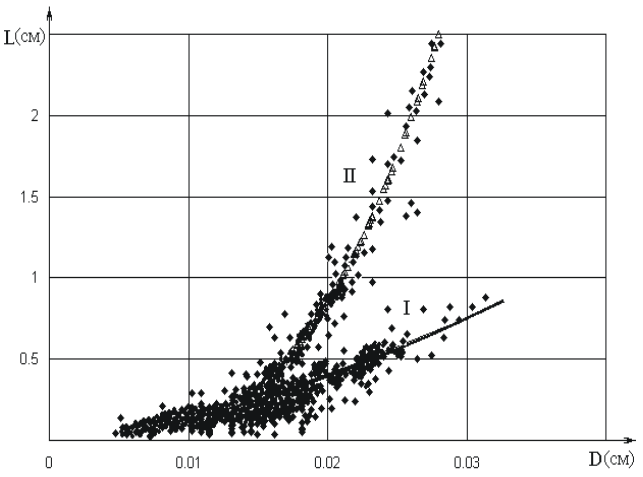

Figure 3: Distribution $L_i(D_i)$, $i = 1-5$ for *Cotinus obovatus* leaf and dependences $L_i = D_i^{1.6}$ (I) and $L_i = D_i^{3.2}$ (II).

The diameters $D_{j,0-2}$ in the bifurcations obey Murray's law with $g \approx 3$. The dependence $m_j(D_{j0})$, where $m_j = (D_{j1}^3 + D_{j2}^3)/D_{j0}^3$ for $j = 1-320$ is presented in Fig.4. The numerical solution of the equation $(1+(D_{j2}/D_{j1})^g)(D_{j1}/D_{j0})^g = 1$ that follows form Murray's law, give $g = 2.59-3.12$ for 37 specimens of *Cotinus obovatus* leaf. For symmetrical dichotomous bifurcations $D_{j1} = D_{j2}$ from Murray's law and (1) one can obtain the recurrent relations $D_i = 2^{1/g} D_{i+1}$, $L_i = 2^{b_2/g} L_{i+1}$. For $g = 3$ it gives the relation $D_i = 2^{1/3} D_{i+1}$ that was used by T.Joung (1809) in the historically first model of a branching

arterial tree. The same relation was obtained for the plant leaf conducting system [11-12].

The relation between the geometry (L_j, D_j) of the separate conducting element and its domain of influence (i.e. the area S_j of the leaf blade region provided with water by this element) was investigated for Cotinus obovatus leaf (Fig.5). The walls of the leaf vessels are permeable and the transporting fluid filters through the pores of the wall into the cells. The linear dependence $\sqrt{S_i} = k_i L_i$ is found out. With regard to (1) hence it follows $S_i = k_i^2 L_i^2 = a_2 k_i^2 L_i D_i^{b_2}$. At $b_2 \sim 1$ we shall obtain $S_i = a_2 k_i^2 \Phi_i /(2p)$, where $\Phi_i = pD_i L_i$ – the lateral surface of the conducting element. This implies that $S_i \sim \Phi_i$ for each conducting element and the balance between inflow of the liquid in the conducting element and the outflow through the lateral surface of an element takes place.

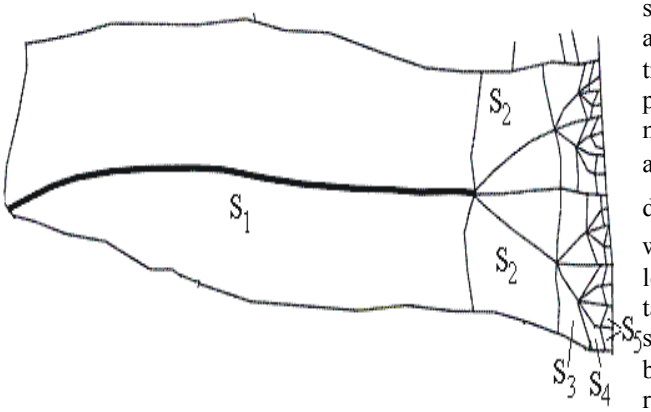

Figure 4: Domains of influence of conducting elements $i = 1-5$ for *Cotinus obovatus* leaf.

The comparative analysis of the data for *Cotinus obovatus* as well as for some other leaves [10,11] and mammalian vascular systems [1-4,6] shows, that both transport structures are characterized by a similar kind of dependences between D_0 and x, D_0 and $a = a_1 + a_2$, D_0 and m. By this means the principles of design of the long-distance transport systems in animals and higher plants are the same.

3. Control over transport systems organization

The arterial system formation in a developing tissue is provided with mechanoreceptors in vascular vessel wall [1,7]. The mechanoreceptors exercise control over network self-organization by maintaining shear rate at the wall t_w in the certain limits [1]. Under steady flow condition (Poiseuille's flow in a cylindrical tube with rigid wall) the shear rate at the wall is $t_w = 32mQ/(pD^3)$. At $t_w = const$ it gives $Q \sim D^3$, that corresponds to the optimal (in the meaning of Murray's law) tube. In such a manner the mechanoreceptors provided the local optimality conditions at each tube in the developing branching vascular tree. For a bifurcation j of the optimal vessels with $Q_{j,0-2} \sim D_{j,0-1}^3$ the continuity condition $Q_{j0} = Q_{j1} + Q_{j2}$, where $Q_{j,0-2}$ - volumetric rate in the tube with diameter $D_{j,0-1}$ leads to the Murray's law for $D_{j,0-1}$ with $g = 3$. Under these circumstances the global optimality conditions for the whole transport system are the same [17] and the transport system possessing the minimal hydraulic resistance at the given total volume develops in the tissue.

The mechanisms of the vein systems with the same geometrical properties formation in plant tissues are unknown yet. The hypothesis of the optimal transport structure formation in plant tissue was proposed in our previous works [18,19]. It based on the model of the branching pipeline with permeable walls and $\Phi_j = nQ_j$ for each tube. At such a condition the diameters D_i of the optimal pipeline with permeable wall obey Murray's law [11,18] and similarity between long-range transport systems in animal and plant tissues takes place. The control over the optimal transport system construction is exercised by alive cells in leaf blade by prevention the vessels' desolation by means of regulation of balance between the plant sap inflow and consumption.

4. Model of optimal bifurcation

Steady motion of a viscous fluid through a single bifurcation (Fig.1) of vessels with permeable walls is considered. Each vessel is represented as thin long round tube ($D_j / L_j << 1$, $j = 0-2$). The mass and impulse continuity conditions in the cylindrical coordinate system at $\mathrm{Re} << 1$ are

$$\frac{1}{r}\frac{\partial}{\partial r}(rV_r) + \frac{\partial V_x}{\partial x} = 0,$$
$$\frac{dp}{dx} = m\left(\frac{\partial^2 V_x}{\partial r^2} + \frac{1}{r}\frac{\partial V_x}{\partial r}\right) \qquad (2)$$

where p – pressure, $V = (V_r, 0, V_x)$ – velocity, m – viscosity of the fluid. The boundary conditions are defined as:

$$V_x\big|_{r=R} = 0, \qquad \left.\frac{\partial V_x}{\partial r}\right|_{r=0} = 0, \qquad V_r\big|_{r=0} = 0, \qquad V_r\big|_{r=R} = w \tag{3}$$

$$p\big|_{x=0} = p_1, \qquad p\big|_{x=L} = p_2 \tag{4}$$

where w - backing-out speed. By integrating (2) with respect to r taking into account (3), we shall receive:

$$V_x = -\frac{1}{4m}\frac{dp}{dx}\left(R^2 - r^2\right)$$
$$V_r = \frac{1}{16m}\frac{d^2p}{dx^2}\left(2R^2 r - r^3\right) \tag{5}$$

and the equation for the pressure field:

$$\frac{d^2p}{dx^2} = \frac{16mw}{R^3} \tag{6}$$

Pressure is obtained from (6), (4) as

$$p^{(1)}(x) = p_1 - Z^p\left(\left(\frac{p_1 - p_2}{Z^p} + \frac{\Phi}{2}\right)y - -\frac{\Phi}{2}y\right) \tag{7}$$

at $w = w_0 = const$ and

$$p^{(2)}(x) = p_1 - Z^p\left(\frac{p_1 - p_2}{Z^p}y + \right.$$
$$\left. + \Phi\left(\frac{2}{3}y - y^2 + \frac{y^3}{3}\right)\right) \tag{8}$$

at $w = 2w_0(1-y)$, where $y = x/L$ or, in other form

$$p^{(1)}(x) = p_1 - Z^p(Qy - \Phi y^2/2)$$
$$p^{(2)}(x) = p_1 - Z^p(Qy - \Phi(y^2 - y^3/3))$$

where $\Phi = pDLw_0$, $Q = 2p\int_0^R rV_x(r,0)dr$, $Z^p = 128mL/(pD^4)$. In both cases of w distribution along the wall the full outflow Φ remains the same. Substitution (7),(8) in (5) gives the velocity fields. Hence it follows that the hydraulic resistance $Z = (p_1 - p(L))/Q$ of the tube are

$$Z^{(1)} = Z^p(1 - \Phi/(2Q)),$$

$$Z^{(2)} = Z^p(1 - 2\Phi/(3Q))$$

For a symmetrical bifurcation ($L_2 = L_1$, $D_2 = D_1$) of the tubes with diameters $L_{0,1}$ and lengths $D_{0,1}$, Poiseuille's law for the tubes in a bifurcation is

$$p_1 - p_2 = Q_1 Z_1, \qquad p_2 - p_3 = Q_2 Z_2$$

where Q_1, $Q_2 = (Q_1 - \Phi_1)/2$, $Z_{1,2}$ – the volumetric rates at the point of entry and hydraulic resistances of the first- and second-order tubes, $p_1 = p(0)$, $p_2 = p(L_1)$, $p_3 = p(L_1 + L_2)$. The x-axis is continuous along two tubes and $x \in [0, L_1]$ for the first-order tube and $x \in [L_1, L_1 + L_2]$ for the second-order ones. Hence it follows for the hydraulic resistance $Z = (p_1 - p_3)/Q_1$ of the bifurcation:

$$Z^{(1)} = Z_1^p + Z_2^p\frac{\Phi_1}{2Q_1}, \quad Z^{(2)} = Z_1^p + Z_2^p\frac{2\Phi_1}{3Q_1}$$

Here $Z = Z(L_{1,2}, R_{1,2}, w_0, Q_1)$ at the constant w_0, Q_1 depends on the bifurcation geometry only. The extreme problem for a bifurcation can be considered in the form of

$$Z(L_{1,2}, R_{1,2}) \to \min, \quad G(L_{1,2}, R_{1,2}) = const \tag{9}$$

where G is a geometrical restriction. Problem (8) for $G = \{V, S, D\}$, where V - full volume, S - full lateral surface, D - full dissipation in the system, and a few other criteria was solved for a single tube and a bifurcation of tubes with non-permeable walls as applied to the arterial vessels. As a result it was obtained that $G = V$ fits the experimental data best of all. Problem (9) with a number of criteria G was solved for a single tube with permeable walls as applied to plant leaves and the same result was obtained [10,11]. Taking into account this conclusion, we consider here the problem (9) with $G = V$ as applied to the bifurcation of tubes with permeable walls. The Lagrange function is $\Xi = Z + lG$. The conditions $\Xi'_{L_{1,2}, R_{1,2}} = 0$ bring finally to the nonlinear system of equations $\{f_i(r,l) = 0\}$, where $r = R_0/R_1$, $l = L_0/L_1$. Here in contrast to the tubes with non-permeable walls the relative diameters and lengths are not independent. The results of the numerical solution of this system are presented in Fig.5. Different curves correspond to the different pairs (Z_j, V) of optimal criteria in (9), where $j = 0$ correspond to the motion in the tube with non-permeable walls, $j = 1,2$ – the tube with permeable walls at $w = w_0 = const$ and $w = 2w_0(1-y)$ respectively. Two dashed lines in Fig.5 correspond to

the upper and lower boundaries of measurement data ($R_0/R_1 \in [1.52;1.91]$, $L_0/L_1 \in [0.22;2.81]$ [10,11]) for a number of leaves with different venation types including *Cotinus obovatus* leaf.

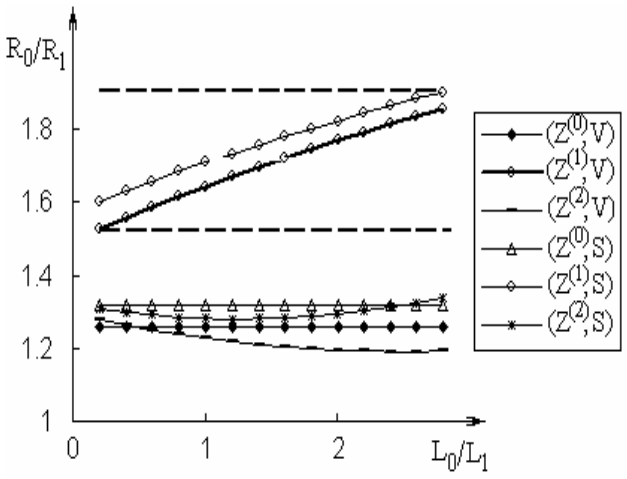

Figure 5: The dependences $R_0/R_1\,(L_0/L_1)$ for the optimal symmetrical bifurcation.

The models of the optimal bifurcation of the tubes with permeable walls both at constant and linearly decreasing functions w agree closely with the measurement data. Two cases of $w(y)$ are differ slightly. For comparison the results of solution of the problem (9) at $G = S$ are presented in Fig.5 as well. All the curves lies closely to the parameters of the optimal bifurcation of tubes with non-permeable walls and do not agree with the measurement data. Consequently the model of optimal bifurcation of the tubes with permeable walls that deliver the liquid with a minimu m hydraulic resistance at a given volume is best suited to the measurement data. This model perfectly corresponds to physics of the sap motion in plant leaves.

5. Modelling of the control over transport system formation in leaves.

In contrast to the tubes with non-permeable walls (blood vessels) the total resistance $Z^{(1,2)}$ depends on the relation between the inflow Q_1 at the point of entry and the outflow Φ_1 through the permeable wall. In the case when $\Phi_1/Q_1 << 1$ or $\Phi_1/Q_1 = const$ in each tube of the branching system the total resistances of the bifurcation differ from $Z^{(0)} = Z_1^p + Z_2^p/2$ by the constant only. Thus the optimal bifurcation of the tubes with the permeable walls will obey the same Murrey's law with $g = 3$ as described in the section 2 and the similarity between the geometry of mammal and plant transport systems take place. The first condition is possible for the 1-2 order vessels but is quite impossible for the last-order vessels where $\Phi_1 \sim Q_1$. The second limitation can underlie the formation of the self-similar transport system in plant leaves.

Unlike the mammal vasculature the plant vessels are empty tubes without alive cell contents so they can not estimate either wall shear stress or any other mechanical parameters. Only the live mesophyll cells in the domains of influence would do that. The possible mechanism can be connected with the balance between the sap amount that is need for all the cells in the domain S_j and the corresponding Φ_j that can be provided by the lateral surface pD_jL_j of the tube.

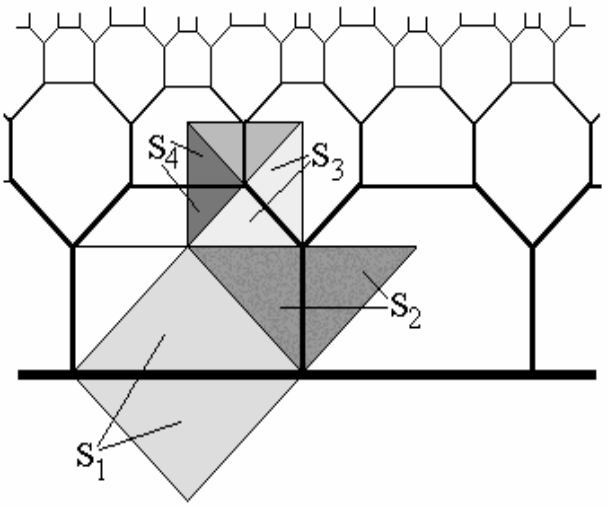

Figure 6: The model of vein system with loops. S_{1-4} – the domains of influence of $j = 1-4$ veins.

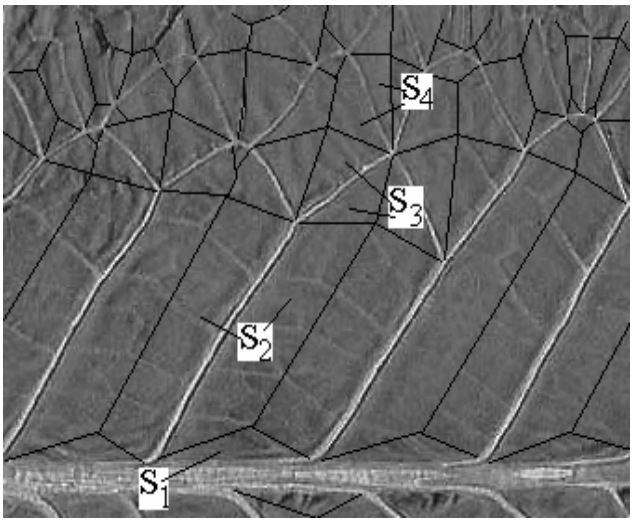

Figure 7: Veins and their domains of influence for Armorasia Rusticana leaf.

Assuming $w_j = S_j / (pD_j L_j)$ the model of the branching system of the tubes with optimal bifurcations where $\Phi_j / Q_j = const$ was constructed (Fig.6). Here $L_0 = 1$, $L_j = 2^{-(n+1)/2}$, $S_j = 2^{-(n+1)}$. The fragment of the venation of Armorasia Rusticana leaf is presented in Fig.7. The model and real vein systems are statistically similar and the only difference is the branching angles between the 1- and 2-order veins ($a_{12} = 90^\circ$ in Fig.6, $a_{12} \sim 42{,}7^\circ$ in Fig.7 [10]).

Conclusions

The branching long-range transport systems in mammal tissues and high plants are statistically identical, obey some relations including well-known Murrey's law and correspond to the model of the optimal pipeline that provided fluid delivering with the minimal cost at a given total volume of the system. The optimization criterion is completely defined by distant liquid transport conditions, even for tree branches where a strength criteria would be more reasonable. The control over the optimal pipeline formation in the developing plant tissue can be connected with the maintenance of the balance between the delivering and consumption, i.e. between form and function.

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